Weed Science 2010 58:147–153

Growth, Phenology, and Intraspecific Competition between Glyphosate-Resistant and Glyphosate-Susceptible Horseweeds (*Conyza canadensis*) in the San Joaquin Valley of California

Anil Shrestha, Bradley D. Hanson, Matthew W. Fidelibus, and Marisa Alcorta*

Experiments were conducted in 2006 to 2008 to study growth, phenology, and competitive ability of glyphosate-resistant (GR) and -susceptible (GS) biotypes of horseweeds from San Joaquin Valley (SJV), CA. When grown alone, in pots, the GR horseweeds consistently developed more rapidly than the GS weeds, as evidenced by their earlier bolting, flowering, and seed set; the GR horseweeds set seeds nearly 25 d (approximately 190 fewer growing degree days) sooner than the GS horseweed. At seed set, the relatively slow-developing GS horseweeds had amassed 40% more shoot dry matter than the GR weeds at the same phenological stage, but neither biotype was consistently more fecund than the other. Although the GR biotype had lower shoot dry mass than the GS biotype when grown alone, in mixed populations under increasing levels of competition (in a replacement series design) and limited resources (mainly moisture), the GR weeds were not only taller, but also accumulated more dry matter than the GS weeds. Thus, the GR biotype was more competitive than the GS biotype, particularly when grown at high densities and under moisture-deficit stress. Therefore, under California conditions there is no apparent fitness penalty for this particular GR horseweed biotype, and it is likely to persist in the environment and outcompete the GS biotypes regardless of further glyphosate selection pressure. If so, this biotype of GR horseweed is likely to become increasingly common in the SJV until effective management strategies are developed and adopted.

Nomenclature: Horseweed, *Conyza canadensis* (L.) Cronq. ERICA.
Key words: Intraspecies competition, glyphosate resistance, phenology, replacement series.

Herbicides used in managed ecosystems exert selection pressure on the mixture of component plant species and biotypes that occur within these systems. Such pressure, if routinely exerted, causes weed population shifts over time and may lead to dominant species that escape, avoid, or are resistant to the herbicides used (Gressel and Segel 1978). Examples of such shifts due to herbicide use have been reported in agroecosystems (Flint et al. 2005; Haas and Streibig 1982; Mahn 1984) and other managed ecosystems (Mahn 1984). There has been increased interest in the study of weed population shifts in glyphosate-tolerant cropping systems (Owen 2008; Reddy 2004; Westra et al. 2008), and systems that rely heavily on glyphosate-based weed control (Powles et al. 1998), because of the popularity in the use of glyphosate and development of glyphosate-resistant (GR) weeds (Owen 2008). Development of effective management strategies for herbicide-resistant weeds requires an understanding of population dynamics and potential impacts of the resistant biotype. For example, some herbicide-resistant biotypes carry a fitness penalty and, in the absence of continued selection with the herbicide, these biotypes will slowly disappear from the population due to reduced competitive ability (Anderson et al. 1996; Holt and Thill 1994). However, in other instances, the mutation conferring resistance does not appear to reduce fitness of the resistant biotype (Holt and Thill 1994; Sibony and Rubin 2002). Therefore, study of the relative fitness and competitive ability of resistant and susceptible biotypes of weeds is of ecological significance and can impact weed management decisions.

Horseweed is a common weed of perennial crops in the San Joaquin Valley (SJV) of California, including vineyards and fruit and nut orchards, and is also commonly found along field margins, roadsides, canal banks, and other noncrop areas. Although present in the region for many years, this weed has recently become a much more prevalent and important pest in perennial crops and surrounding areas (Hanson et al. 2009). For a variety of reasons, including economics, groundwater protection regulations, and ease of weed management, many California producers of orchard and vineyard crops have switched from weed management strategies based on tillage and pre-emergence herbicides to postemergence herbicide programs, often using repeated applications of glyphosate (Shrestha et al. 2007). For example, from 2002 to 2007 the proportion of hectares treated with glyphosate increased from 81 to 110% in stonefruit orchards and from 116 to 144% in tree nut crops, indicating multiple applications per year in many cases, and similar increases in glyphosate use were noted in citrus orchards during the same period (California Department of Pesticide Regulation [CADPR] 2009). In 2007, the first case of GR horseweed was reported in California (Shrestha et al. 2007).

Because there are numerous cases of GR weeds, including horseweed, in other cropping systems that rely on repeated applications of glyphosate around the world (Heap 2009), selection for a GR biotype in California perennial crops should be of no surprise. The abundance and distribution of the GR biotype in the region; however, was somewhat surprising. In a survey conducted in 2006 and 2007, the majority of horseweed plants sampled in the southern SJV were GR, regardless of nearby cropping systems (Hanson et al. 2009), suggesting the possibility that increased fitness may have contributed to the very rapid expansion in the range of the GR biotype.

DOI: 10.1614/WS-D-09-00022.1
* Department of Plant Science, California State University, 2415 East San Ramon Avenue, MS A/S 72, Fresno, CA 93740; U.S. Department of Agriculture, Agricultural Research Service, 9611 South Riverbend Avenue, Parlier, CA 93648; Department of Viticulture and Enology, University of California, Davis, Kearney Agricultural Center, 9240 South Riverbend Avenue, Parlier, CA 93648; Department of Viticulture and Enology, University of California, One Shields Avenue, Davis, CA 95616. Current address of second author: Department of Plant Sciences, University of California, One Shields Avenue, Davis, CA 95616. Corresponding author's E-mail: ashrestha@csufresno.edu

Other researchers have found substantial differences among competitive abilities of *Conyza* spp. (Thebaud et al. 1996). However, little information is available on the fitness costs or benefits related to glyphosate resistance in horseweed (Powles and Preston 2006). Observations of vigorous and productive GR horseweed, regardless of whether it is growing in treated or untreated areas, suggests that the GR horseweed in California may be more competitive than the glyphosate-susceptible (GS) biotype in addition to being resistant to the most commonly used herbicide in orchards, vineyards, and adjacent noncrop areas (Shrestha, personal observation). Studies showed that the GR horseweed biotype possessed early vigor compared to GS biotypes (Grantz et al. 2008; Shrestha et al. 2007). These findings may have ecological significance to the population dynamics of these two biotypes of horseweed in the SJV. Therefore, the objectives of this study were to determine the phenological development of GR and GS horseweed and to determine their relative competitive ability in the absence of glyphosate applications.

Materials and Methods

Growth and Phenological Development. Seeds from two previously characterized (Hanson et al. 2009; Shrestha et al. 2007) horseweed biotypes from Fresno County (36°47′58″N; 119°57′16″W) and Tulare County (36°29′15″N; 119°24′10″W), CA, were used to determine the differences in growth and phenological development of GR and GS horseweed. At the rosette stage, plants grown from seeds collected from Tulare County survived a glyphosate application rate of 4.4 kg ae ha^{-1}, whereas, at the same growth stage, plants from Fresno County were susceptible to 1.1 kg ae ha^{-1} of glyphosate. Seeds were scattered onto the surface of moist potting mix[1] in 26 by 52 by 6–cm plastic seedling trays.[2] Each tray was covered with a transparent plastic dome to maintain humidity. The trays were placed in a no-hole runoff catchment tray, and placed onto a heated (26 C) seed germination mat[3] under ambient laboratory fluorescent lighting (10 μmol m^{-2} s^{-1}). Water was added to the catchment tray for subirrigation. Seeds were planted on March 14, March 6, and February 26, in 2006, 2007, and 2008, respectively. Seeds from the original collection were used in each year of the study. After seedling emergence, the trays were transferred to a greenhouse at the University of California Kearney Research and Extension Center for acclimation. Seedlings of similar size (two to three true leaf stage) were selected and transplanted to a separate black polyethylene pot containing about 8 L of commercial growth media[4] (6 : 2 : 1 : 1; sphagnum peat moss : ground conifer bark : compost : sand). The seedlings were transplanted on April 12, April 2, and March 19, in 2006, 2007, and 2008, respectively. Plants were grown in pots to reduce the potential for soil variables affecting the study. The pots were moved outdoors in the full sun immediately after transplant. The plants were hand watered regularly, and no supplemental fertilizer was added during the experiment. Plant height measurements (main stem only) were made at weekly intervals after transplanting and on the day of plant harvest. The plants were visually inspected on alternate days for formation of a rosette (more than 20 leaves), bolting (extension of the main stem), first appearance of a floral bud, first appearance of an open flower, and first appearance of a flower with seeds. Initial dates for each of these events for each plant were recorded. A plant was harvested as soon as the first appearance of a flower with seeds, to ensure harvesting of the plants at the same phenological stage. Thus, the harvest date of the plants varied and ranged from 16 to 20 wk after transplanting (WAT), depending on the biotype and the year. The plants were clipped at the surface of the soil, bagged, and transported to the laboratory. In the laboratory, the leaves, stems, flowers, and buds were separated and put into paper bags and dried in a forced-air oven at 70 C for 72 h. The dry weight of each sample was measured and recorded. The flowers and buds on each plant were counted before being put into the paper bags. Five seed heads were randomly selected from each plant and dissected by hand, and the seeds were counted. The total number of seeds on a plant was estimated as the number of flowers multiplied by the average number of seeds in the five seed heads.

The experiment was arranged as a completely randomized design with the two biotypes (GR and GS) as fixed effects and year as a random effect. Each plant was considered a replicate. There were four replications in 2006 and 2007, and five replications in 2008. Data for elongation of main stem and phenological development over the growing season was initially expressed as a function of days after transplanting (DAT). These variables were also modeled as a function of growing degree day (GDD). The corresponding cumulative GDD at each DAT were calculated as ([daily maximum temperature + daily minimum temperature]/2 − T_b) from time of emergence, where the base temperature (T_b) of horseweed was considered 13 C based on the studies of Steinmaus et al. (2000).

Data were tested for normality and analysis of variance (ANOVA) was performed with the GLM procedure in SAS.[5] No interactions ($P > 0.05$) occurred between year and biotype for any of the parameters. Therefore, data for the measured and estimated parameters were combined for the 3 yr. Rate of main-stem elongation was regressed against GDD with the use of a three-parameter logistic function (Equation 1) (Brown and Mayer 1988):

$$Y = a/1 + \left(x/x^0\right)^b, \qquad [1]$$

where Y is the main-stem length, a is the upper asymptote (maximum), x is the GDD, x_0 is the GDD when Y is 50% of the maximum (median), and b is the slope at x_0. The logistic model was fit with the use of SigmaPlot.[6] This model provided the best fit to the data ($r^2 > 0.80$).

Relative Competitive Ability. The same previously characterized horseweed biotypes were also used to determine the relative competitive ability between GR and GS horseweed. In February 2006 and March 2007, seed from each field collection was sown on the surface of commercial potting media[7] in 26 by 52 by 6–cm plastic trays[2] in a greenhouse and moist soil conditions were maintained with daily drip irrigation. After emergence, single seedlings were transferred into peat pellets[8] and grown to approximately a 5-cm rosette size in the greenhouse. After reaching sufficient size and being acclimated to outdoor temperatures, seedlings were transplanted in March 2006 and April 2007 into 40 L (38 cm diam by 38 cm deep) pots filled with a 1 : 3 v/v mixture of perlite and steam-sterilized field soil (Hanford sandy loam).

Horseweed rosettes were transplanted according to an addition series experimental design with five GR : GS ratios,

three population densities, and four replicates. Plants in each pot were arranged in 2 by 2, 3 by 3, or 4 by 4 grids (Jollife 2000) to achieve final planting densities of 4, 9, and 16 plants pot^{-1} or 36, 82, and 145 plants m^{-2}, respectively. These levels of horseweed infestation are not uncommon in irrigated areas in central California, especially early in the growing season. GR : GS planting ratios of 0 : 100, 25 : 75, 50 : 50, 75 : 25, and 100 : 0 were used at each population level and each individual GR and GS horseweed plant was marked with plastic stakes or ribbons to ensure proper identification throughout the experiment. In the nine plants pot^{-1} density, planting ratios were based on eight plants and a ninth plant was randomly assigned to either a GR or GS horseweed to complete the planting grid.

After transplanting, plants were irrigated twice daily with a single 1.9 L hr^{-1} drip irrigation emitter in the center of each pot to maintain moist soil conditions during establishment. Beginning 1 WAT, an individual GR and/or GS plant near the center of each pot was marked for weekly measurement. Dead plants were replaced with similar-sized plants for the first 3 WAT. The horseweed plants tolerated transplanting very well, with only 0.3 to 1.9% replaced during the first 3 wk, only one of which was a plant marked for weekly measurements. After horseweed rosettes were well established, the daily irrigation was reduced on a replicated set of each density/ratio treatment combinations in order to evaluate relative competitive ability under high and low water stress. The original goal of the water treatments was to use reference evapotranspiration (ET) data collected at a nearby California Irrigation Management Information System[9] (CIMIS) weather station to determine daily irrigation needed to replace 90 and 180% of the calculated water losses at each irrigation level. However, after 1 mo of irrigation treatments in 2006, it was clear that reference ET values were not representative of horseweed water use under these conditions, because even the plants grown at low density under the high water level had visual water stress symptoms. Thus irrigation treatments were ramped up over a 1-mo period from approximately 90 to 204% of ET in the low water treatment and from 183 to 424% of ET in the high water treatment in 2006. Similarly, in 2007 water treatments ramped from 86 to 264% ET in the low water level and from 177 to 363% ET in the high water treatment during the course of the experiment. The irrigation system was set to deliver half of the allotted water to each pot in the early morning and half in the late afternoon. This regime usually resulted in minor afternoon leaf wilting of plants grown under low water and high planting density conditions.

Main-stem height of the marked GR and GS horseweed near the center of each pot was measured weekly throughout the summer growing season until the earliest plants began flowering. At flowering, the experiment was terminated and total above- and below-ground biomass yield for each biotype was determined by removing the plants from each pot. Surviving GR and GS plants in each pot were counted, soil was washed from the root system, roots were clipped from the shoots, and biomass was oven dried to constant weight at 50 C and weighed to determine total root and shoot biomass yield for each biotype. Effects of planting density, irrigation level, and year were determined with the use of analysis of variance, and means were separated with the use of Fisher's Protected LSD procedures. Additionally, 95% confidence intervals were calculated and used to compare relative biomass yield to predicted biomass yield if the biotypes were equally competitive.

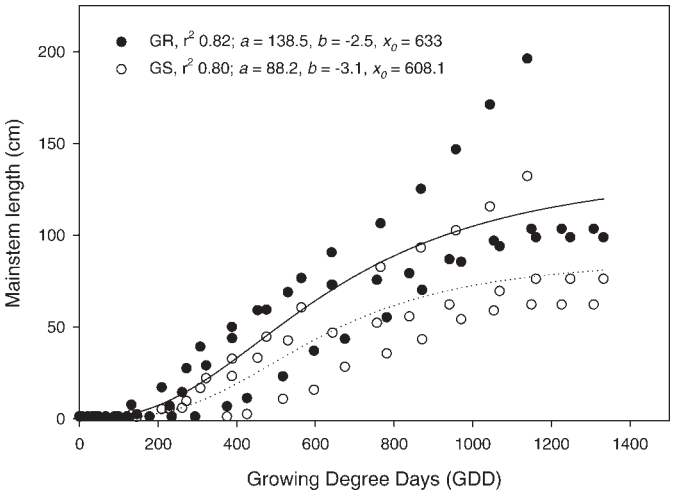

Figure 1. Main-stem length of glyphosate-resistant (GR) and glyphosate-susceptible (GS) horseweed as a function of growing degree days (GDD) averaged for the 3 yr. The solid line and dotted lines represent the three-parameter logistic curves fit to the GR and GS biotypes, respectively.

Results and Discussion

Main-Stem Elongation. In the absence of competition, the GR biotype was taller than the GS biotype at all the sampling dates, beginning approximately 1 mo after transplanting. Main-stem elongation as a function of GDD showed that the GR biotype elongated more rapidly than the GS biotype (Figure 1). Main-stem elongation when modeled as a function of GDD showed r^2 values of 0.82 and 0.80 for GR and GS biotypes, respectively. All plants, regardless of biotype, were taller in 2008 than in previous years, possibly because they were transplanted sooner in 2008 than in the other 2 yr. The GS biotype in all 3 yr of the study took longer to bolt than the GR biotype. This caused the initial difference in main-stem length, and this difference persisted for the duration of the growing season. Although this study showed that the GR biotypes were taller than the GS biotypes as a result of earlier bolting, it cannot be ascertained if the final height of the two biotypes would have been different. Horseweed plants in this study were harvested as soon as a seed with a pappus was observed on each individual plant; thus, the plants were not allowed to complete the entire growth cycle. It has been observed (Shrestha, personal observation) that horseweed plants elongate even after the formation of some mature seeds with pappus. Regardless of potential end-of-season height differences, this study clearly showed that main-stem elongation started earlier and was more rapid in the GR than in the GS biotype, as previously reported (Grantz et al. 2008). Such differences in early vigor and main-stem elongation can have an ecological significance when the two biotypes are growing together. The GR and GS horseweed biotypes are commonly found growing together in the SJV (Hanson et al. 2009) and further mixing of biotypes is likely to occur, because seeds of horseweed have been known to travel as far as 300 miles on wind currents (Shields et al. 2006).

Plant Biomass. The GS biotype accumulated approximately 40% more shoot dry matter than the GR biotype by the onset of seed set on plants grown with no competition (Table 1). The plants accumulated more dry matter in 2008 than in 2006 or 2007, but the relative difference in mass between the

Table 1. Total aboveground biomass of glyphosate-resistant (GR) and glyphosate-susceptible (GS) plants grown in full sun in 2006, 2007, and 2008. Data were averaged across years.

Biotype	Leaf[a]	Stem[a]	Flowers[a]	Aboveground biomass[a]
	g plant^{-1}			
GR	27.1 b	71.1 a	5.7	103.9 b
GS	39.5 a	99.9 a	5.8	145.2 a
P value biotype	0.004	0.057	0.615	0.011
P value year	< 0.0001	0.003	0.009	< 0.0001
P value year × biotype	0.12	0.2374	0.006	0.06

[a] Means within a column for biotype followed by the same letter are not different according to Student's *t* test at P = 0.05.

two biotypes was consistent each year. Averaged over the 3 yr, the GS plants produced more leaf and stem dry matter (P = 0.057) than the GR plants. Because the main-stem length was greater in the GR than the GS biotype but the GS biotype produced more biomass, it is very likely that the GS biotype had heavier or more stems per plant than in the GR biotype. Although the GR biotype had less shoot dry matter, both biotypes produced similar flower dry matter, and the number of flowers and seeds varied among years and biotypes such that there were no consistent trends in fecundity (Table 2). Davis et al. (2009) found no differences in seed production or biomass between the GR and GS biotypes of horseweed, suggesting no fitness penalty for the GR biotype. Based on our data, the GS biotype can be characterized as shorter and leafier plants with heavier or more stems compared to the GR biotype. Such differences between biotypes in plant architecture can be of significance for control of these species with postemergence herbicides.

Phenological Development. The GR biotype exhibited accelerated phenological development compared to the GS biotype (Table 3). Although the two biotypes formed a rosette at a similar time, the GR biotypes bolted, formed floral buds, flowered, and set seeds earlier than the GS biotype. First seed formation was observed approximately 3 to 4 wk earlier in the GR than in the GS biotype. Similar phenomena were reported in common lambsquarters (*Chenopodium album* L.), where the GR biotypes initiated floral primordial 4 to 6 wk before the GS biotypes (Westhoven et al. 2008). There was a significant effect of year on the phenological development of the plants, but no year-by-biotype interaction. In terms of cumulative thermal time, the GR biotype required fewer GDDs than the GS biotype to reach the various growth stages. Visual observations suggested that the GS plants had longer and more leaves at the rosette stage than the GR biotype. These differences in phenology may affect the success of postemergence herbicide applications based simply on the time of year or crop growth stage. At a given time of year, the GR biotype may be at a more advanced stage of phenological development than the GS biotype at the time of postemergence herbicide application. Previous research has shown that both GR and GS horseweed is more tolerant of glyphosate at later growth stages (Shrestha et al. 2007) and the same may be true for other herbicides. Therefore, differences in plant phenology may have to be taken into consideration when developing horseweed management strategies. Although it may be impractical to do so because these biotypes occur together in agroecosystems, early application may ensure better control than later applications of postemergence herbicides because GR biotypes could be taller and at an advanced phenological stage if treatment is delayed.

Relative Competitive Ability. Difficulties related to precise control of water stress treatments were encountered in this experiment. Irrigation treatment levels much higher than reference ET values were needed to minimize visual symptoms of drought stress, which suggests that horseweed uses relatively more water than many crop plants or, more likely, that a significant proportion of the irrigation water was lost from the system due to percolation though the soil or channeling between the pot and soil. Results of a preliminary experiment indicated that a 1 : 3 mixture of perlite and field soil was a good compromise for increasing water-holding capacity over field soil; however, these results did not account for changes in physical properties after several months in pots in an arid environment. Additionally, short, frequent irrigations may have resulted in relatively higher evaporative water losses from the surface of the soil relative to transpiration losses. Because the actual soil moisture levels in this experiment cannot be known with certainty, the results from the irrigation main effect should be interpreted on a relative scale as being due to lower and higher stress rather than unstressed and stressed growing conditions. There was a significant effect of year on height of both horseweed biotypes at nearly every weekly measurement (P < 0.05) (data not shown). This effect may have been influenced by the planting schedule and environmental differences between years. Seedlings in 2006 were started several weeks later compared to 2007, and were somewhat smaller when moisture stress regimes were initiated. Although the main effect of year was significant, the two-way interactions involving year were rarely significant. When the ANOVA for each weekly measurement was rerun and averaged over years, only high population densities reduced height prior to initiation of water stress treatments 4 WAT. However, beginning 5 WAT, the main effects of water level, population density, and biotype significantly affected horseweed height throughout the remainder of the experiment (P < 0.05). Main-stem length at the end of the experiment indicated that, in general, the GR biotype was taller than the GS biotype regardless of planting density or water regime

Table 2. Total seed and flower production in the glyphosate-resistant (GR) and glyphosate-susceptible (GS) plants grown in full sun in 2006, 2007, and 2008.

Biotype	Flowers[a]			Seeds[a]		
	2006	2007	2008	2006	2007	2008
	No. plant^{-1}					
GR	9,979 a	3,440 b	2,216 a	792,799 a	191,842 b	144,033 a
GS	4,778 b	7,082 a	2,973 a	400,771 b	429,614 a	193,245 a
P value	0.047	0.05	0.172	0.03	0.040	0.172

[a] Means within a column followed by the same letter are not different according to Student's *t* test at P = 0.05.

Table 3. Average time for glyphosate-resistant (GR) and glyphosate-susceptible (GS) horseweed to reach various phenological stages in terms of days after transplanting (DAT) and the corresponding growing degree days (GDD). Data were averaged over years.

	Biotype				
	GR		GS		
Phenological stage	DAT[a] (± SE)	GDD[b] (± SE)	DAT[a] (± SE)	GDD[b] (± SE)	P value
Rosette	37 (3) A	123 (13) a	36 (2) A	122 (17) a	0.59
Bolting	56 (3) B	268 (23) b	65 (3) A	350 (37) a	0.004
First bud	128 (5) B	1,280 (43) b	148 (4) A	1,457 (52) a	0.002
First flower	138 (5) B	1,379 (41) b	160 (5) A	1,571 (43) a	0.002
First seed	146 (6) B	1,479 (35) b	171 (5) A	1,671 (33) a	0.001

[a] Means within a row followed by the same upper- or lower-case letters are not different according to Student's *t* test at P = 0.05.
[b] Growing degrees days calculated with a base temperature of 13 C.

(Figure 2). Height of both biotypes was reduced similarly by high planting density and low irrigation level. Planting ratio had no effect on the height of horseweed during these addition series experiments. In 2006, although usually shorter, both horseweed biotypes produced more biomass than in 2007 (Figure 3). A significant year by biotype interaction was observed in shoot dry matter production such that the GR biotype produced more dry matter than GS in 2006 but the two biotypes were similar in 2007 (Figure 3). However, when the dry matter was converted to relative biomass (relative to the same biotype grown at the same density in monoculture), year was not significant and substantial differences among biotype were noted (Figure 4). Compared to the expected biomass production, if the biotypes were equivalently productive (dashed lines in Figure 4), the GR response was usually convex, whereas the GS response was slightly concave, which indicates that the GR biotype used in the experiment has a competitive edge over the GS biotype (Radosevich et al. 1997). This effect was least noticeable at the high water level and lowest planting density, which suggests that, under low-stress agricultural situations, GS and GR plants may be similarly productive.

Overall, this research indicated that this particular GR horseweed biotype of central California differed in early-season growth, phenology, and competitive ability compared to the GS biotype in the absence of glyphosate. The GR horseweed required fewer GDD to reach each vegetative and reproductive stage. When grown with no inter- or intraspecific competition, the GR biotype grew taller than GS biotype, but the GS biotype tended to produce slightly more leaf and stem biomass. However, reproductive capability did not appear to differ between the two biotypes grown under low-stress, no-competition environments. Conversely, when grown in mixed populations under increasing levels of competition and limited resources, the GR biotype grew taller and larger, likely due to more rapid early-season growth and resource capture. Under California crop and noncrop conditions there is no apparent fitness penalty for this particular GR horseweed biotype, and it is likely to persist in the environment. Given the ecological ramifications of equal or greater fitness in GR horseweed and the continued reliance of growers, land managers, and homeowners on glyphosate, this GR horseweed biotype is likely to become an even larger management problem in the SJV unless alternative management strategies are developed and adopted. However, more studies on additional GR and GS horseweed biotypes need to be conducted to ascertain whether these findings hold true for all GR and GS biotypes, because studies in rigid ryegrass (*Lolium rigidum* Gaud.) have found that considerably variability occurred in herbicide (aroloxyphenoxypropionate and sulfonylurea) -resistant and -susceptible biotypes in their

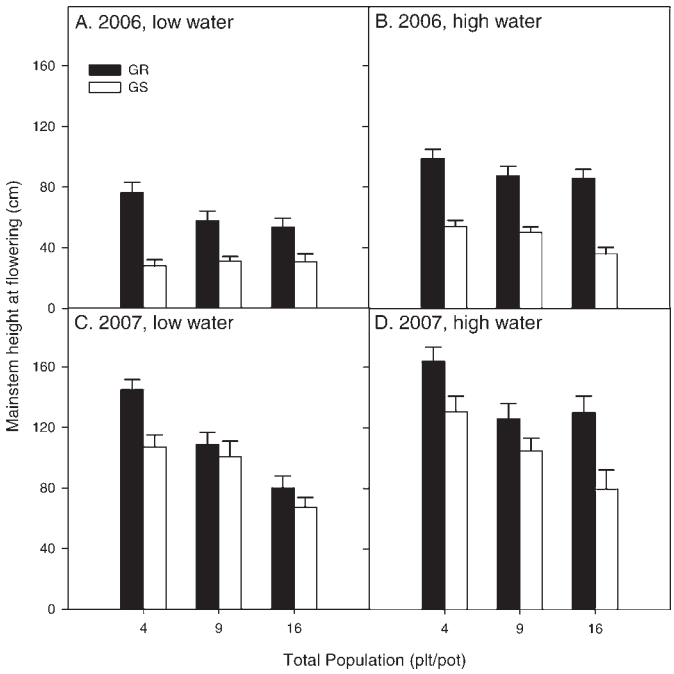

Figure 2. Effect of water stress, and plant population on main-stem height of glyphosate-resistant (GR) and -susceptible (GS) horseweed grown in an addition series experiment in 2006 and 2007. Data are means and 95% confidence intervals based on four replicates at each treatment combination.

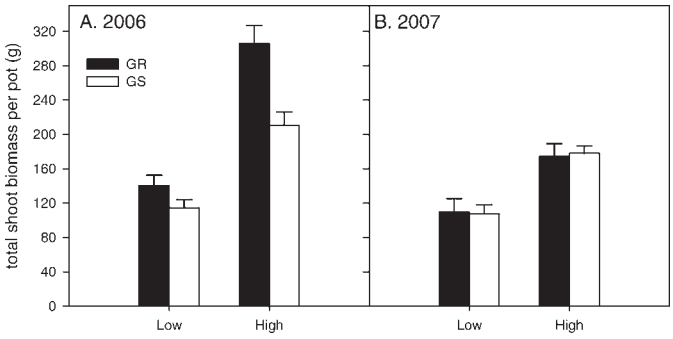

Figure 3. Effect of water stress on aboveground biomass production of glyphosate-resistant (GR) and -susceptible (GS) horseweed grown in monoculture in an addition series experiment in 2006 and 2007. Data are means and 95% confidence intervals averaged over three planting densities (4, 9, and 16 plants pot^{-1}) and four replicates.

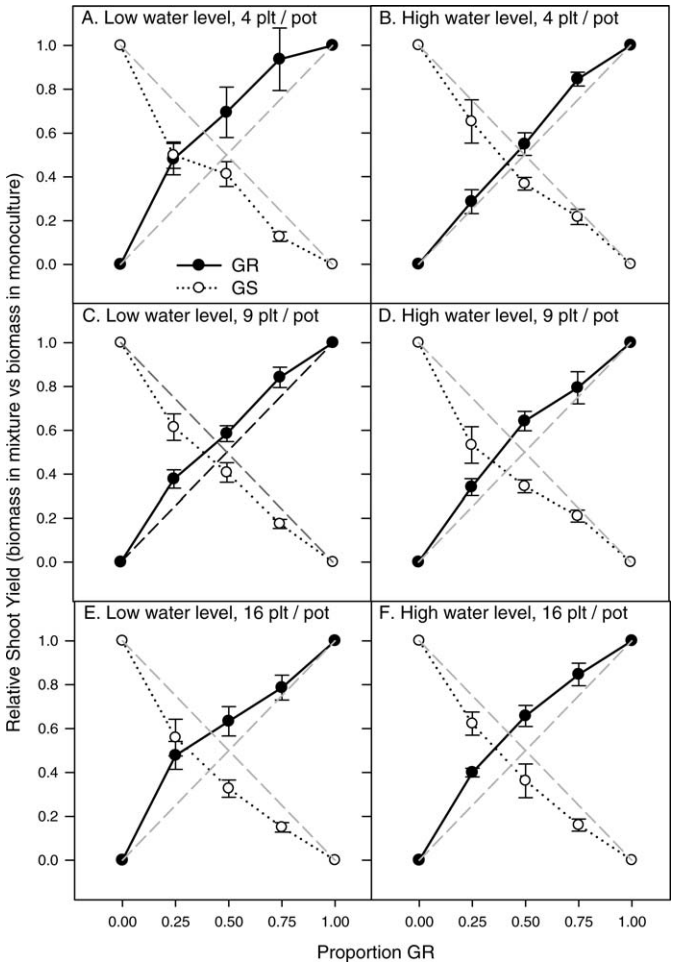

Figure 4. Relative aboveground biomass of glyphosate-resistant (GR) and -susceptible (GS) horseweed grown in an addition series experiment in 2006 and 2007. Lines and symbols represent biomass in each plot relative to the same biotype grown in monoculture at each population density, and dashed lines indicate the expected biomass production if the biotypes were equally competitive. Error bars are 95% confidence intervals.

relative growth rate and phenological development (Gill et al. 1996).

Sources of Materials

[1] Potting mix, Pro Mix BX, Premier Horticultural Products, Oceanside, CA 92054.

[2] Seeedling trays, 28 by 55 by 5 cm, TLC Polyform, Hummert International Inc., Earth City, MO 63045.

[3] Seedling heat mat, Hydrofarm, 2249 South Mcdowell Ext., Petaluma, CA 94954.

[4] Commercial growth media Supersoil®, Scott's Miracle-Gro Co., 914 South Claremont Street, San Mateo, CA 94402.

[5] [SAS] Statistical Analysis Systems Institute, Inc., Cary, NC 27512-8000.

[6] SigmaPlot (version 9 for windows), Systat Software, Inc., 501 Canal Boulevard, Suite C, Point Richmond, CA 94804-2028.

[7] Commercial potting media, Metro-Mix 200, Sun Gro Horticulture, Inc., 15831 NE 8th Street, Suite 100, Bellevue, WA 98008.

[8] Jiffy-7 peat pellets, Jiffy Products of America Inc., 600 Industrial Parkway, Norwalk, OH 44587.

[9] California Irrigation Management Information System (CIMIS). Available at: http://wwwcimis.water.ca.gov/.

Acknowledgments

The authors gratefully acknowledge the technical assistance of Stella Zambrzuski, Karen Pelham, Idalia Orellana, Ashley Torres, Kimberley Cathline, Melissa Chavez, Socorro Cisneros, Lydia Cisneros, Jorge Aguilar, Thomas Wang, Ivan Ramirez, Kurt Hembree, and Neil Va. Partial funding for student interns was received from the Louis Stokes Alliance for Minority Participation Program, the U.S. Department of Agriculture, Agricultural Research Service, Pacific West Area Summer Intern Program, the Fruit Tree, Nut Tree, and Grapevine Improvement Advisory Board, the Garden Rose Council, and the University of California Statewide Integrated Pest Management Program competitive grants program.

Literature Cited

Anderson, D. D., L. G. Higley, A. R. Martin, and F. W. Roeth. 1996. Competition between triazine-resistant and -susceptible common waterhemp (*Amaranthus rudis*). Weed Sci. 44:853–859.

Brown, R. F. and D. G. Mayer. 1988. Representing cumulative germination. The use of the Weibull function and other empirically derived curves. Ann. Bot. 61:127–138.

[CADPR] California Department of Pesticide Regulation. 2009. Pesticide Use Reporting Database. http://www.cdpr.ca.gov/docs/pur/purmain.htm.

Davis, V. M., G. R. Kruger, J. M. Stachler, M. M. Loux, and W. G. Johnson. 2009. Growth and seed production of horseweed (*Conyza canadensis*) populations resistant to glyphosate, ALS-inhibiting, and multiple (glyphosate + ALS-inhibiting) herbicides. Weed Sci. 57:494–504.

Flint, S. G., D. R. Shaw, F. S. Kelley, and J. C. Holloway. 2005. Effect of herbicide systems on weed shifts in soybean and cotton. 2005. Weed Technol. 19:266–273.

Gill, G. S., R. D. Cousens, and M. R. Allan. 1996. Germination, growth, and development of herbicide resistant and susceptible populations of rigid ryegrass (*Lolium rigidum*). Weed Sci. 44:252–256.

Grantz, D. A., A. Shrestha, and H. Vu. 2008. Early vigor and ozone response in horseweed (*Conyza canadensis*) biotypes differing in glyphosate response. Weed Sci. 56:224–230.

Gressel, J. and L. A. Segel. 1978. The paucity of plants evolving genetic resistance to herbicides: possible reasons and implications. J. Theor. Biol. 75:347–377.

Haas, H. and J. C. Streibig. 1982. Changing patterns of weed distribution as a result of herbicide use and other agronomic factors. Pages 57–97 *in* H. M. Lebaron and J. Gressel, eds. Herbicide Resistance in Plants. New York: John Wiley & Sons.

Hanson, B. D., A. Shrestha, and D. Shaner. 2009. Distribution of glyphosate-resistant horseweed (*Conyza canadensis*) and relationship to cropping systems in the Central Valley of California. Weed Sci. 57:48–53.

Heap, I. 2009. The International Survey of Herbicide Resistant Weeds. www.weedscience.com. Accessed: August 6, 2009.

Holt, J. S. and D. C. Thill. 1994. Growth and productivity of resistant plants. Pages 299–316 *in* S. B. Powles and J.A.M. Holtum, eds. Herbicide Resistance in Plants: Biology and Biochemistry. Boca Raton, FL: CRC Press.

Jolliffe, P. A. 2000. The replacement series. J. Ecol. 88:371–385..

Mahn, E. G. 1984. Structural changes of weed communities and populations. Vegetatio 58:79–85.

Owen, M.D.K. 2008. Weed species shifts in glyphosate-resistant crops. Pest Manag. Sci. 64:377–387.

Powles, S. B., D. F. Lorraine-Colwill, J. J. Dellow, and C. Preston. 1998. Evolved resistance to glyphosate in rigid ryegrass (*Lolium rigidum*) in Australia. Weed Sci. 46:604–607.

Powles, S. B. and C. Preston. 2006. Evolved glyphosate resistance in plants: biochemical and genetic basis of resistance. Weed Technol. 20:282–289.

Radosevich, S., J. Holt, and C. Ghersa. 1997. Weed Ecology: Implications for Management. 2nd ed. New York: John Wiley & Sons. 589 p.

Reddy, K. N. 2004. Weed control and species shift in bromoxynil- and glyphosate-resistant cotton. Weed Technol. 18:131–139.

Shields, E. J., J. T. Dauer, M. J. VanGessel, and G. Neumann. 2006. Horseweed (*Conyza canadensis*) seed collected in the planetary boundary layer. Weed Sci. 54:1063–1067.

Shrestha, A., K. J. Hembree, and N. Va. 2007. Growth stage influences level of resistance in glyphosate-resistant horseweed. Calif. Agric. 61(2):67–70.

Sibony, M. and B. Rubin. 2003. The ecological fitness of ALS-resistant *Amaranthus retroflexus* and multiple-resistant *Amaranthus blitoides*. Weed Res. 43:40–47.

Steinmaus, S. J., T. S. Prather, and J. S. Holt. 2000. Estimation of base temperatures for nine weed species. J. Exp. Bot. 51:275–286.

Thebaud, C., A. C. Finzi, L. Affre, M. Debussche, and J. Escarre. 1996. Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean oil fields. Ecology 77:791–804.

Westhoven, A. M., G. R. Kruger, C. K. Gerber, J. M. Stachler, M. M. Loux, and W. G. Johnson. 2008. Characterization of selected common lambsquarters (*Chenopodium album*) biotypes with tolerance to glyphosate. Weed Sci. 56:685–691.

Westra, P., R. G. Wilson, S. D. Miller, P. W. Stahlman, G. W. Wicks, P. L. Chapman, J. Withrow, D. Legg, C. Alford, and T. A. Gaines. 2008. Weed population dynamics after six years under glyphosate- and conventional herbicide-based weed control strategies. Crop Sci. 48:1170–1177.

Received August 16, 2009, and approved November 19, 2009.